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A Study of the Biology and Behavior of the Caterpillars, Pupae and Emerging Butterflies of the Subfamily Heliconiinae in Trinidad, West Indies. Part II. Molting, and the Behavior of Pupae and Emerging Adults[1,2]

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(Plate I; Text-figures 1-3)

CONTENTS

I. INTRODUCTION

A PRELIMINARY STUDY has been made of the behavior of as many species of larval heliconiines as were available over a period of 4½ months spent in Trinidad, W. I. A comparative account of the general activities, such as feeding, resting, locomotion and social and defensive behavior, has already been given (Alexander, 1961). Observations on the late larvae, however, made it clear that some of the significance of their behavior should be sought in the pupa and emergent adult. Hence descriptions of some of these aspects of heliconiine behavior are presented here as Part II of the report, together with observations on molting behavior throughout larval life.

The information relates to eleven of the fourteen species of heliconiines found in Trinidad, namely *Heliconius doris doris* (Linnaeus), *Heliconius sara thamar* Hubner, *Heliconius erato hydara* Hewitson, *Heliconius melpomene euryades* Riffarth, *Heliconius ricini insulana* Stichel, *Heliconius aliphera aliphera* (Godart), *Heliconius isabella isabella* (Cramer), *Dryadula phaetusa phaetusa* (Linnaeus), *Dryas iulia iulia* (Fabricius), *Agraulis vanillae vanillae* (Linnaeus) and *Dione juno juno* (Cramer).

Descriptions and illustrations of the external characteristics of the larvae referred to here are given by Beebe, Crane & Fleming (1960).

TABLE I. MOLTING BEHAVIOR IN SPECIES OF HELICONIINE CATERPILLARS
Records of times abstracted from approximately three cases for each species, but confirm
general impressions of molts whose details were not recorded.

Species	Position on vine prior to molt	Pose prior to shedding skin	Time of day when skin normally shed
Dione juno	Stem	Arranged in circle, heads to center, bodies straight	Mid-a.m.
Agraulis vanillae	Midrib/stem	–	Mid-a.m. to mid-p.m.
Dryas iulia	Midrib/stem/ tendril	"J"/straight	Mid-a.m. to early p.m.
Dryadula phaetusa	Midrib	"J"/straight	Noon to early p.m.
Heliconius aliphera	Midrib	Curved	Mid-a.m.
Heliconius isabella	Leaf blade	Straight	p.m.
Heliconius melpomene	Midrib	Straight/head slightly to one side	Mid-a.m. to early p.m.
Heliconius erato	Stem, seldom midrib	Straight	Mid-a.m.
Heliconius ricini	Midrib/stem	?	Mid-a.m.
Heliconius sara	Stem, few on leaves	Straight	Early a.m. to noon

II. MOLTING BEHAVIOR

As in most butterflies, the Heliconiinae typically have four molts separating five larval stages. Six instars may occur occasionally in some species—*H. sara, H. isabella, H. aliphera* and to a lesser extent *H. melpomene* and *D. juno* (Beebe, Crane & Fleming, 1960).

Normal molting is very similar in all species observed and a generalized description will be given first.

During the afternoon before a caterpillar actually sheds its skin, it selects a site and takes up a position ready for molting, both of these actions varying slightly from species to species (Table I). The caterpillar rests with thorax sharply arched into the air and head bowed down. During this period the dorsal skin between the prothorax and head capsule becomes enormously stretched and a pale band appears beneath it—the new head capsule showing through the old skin. It is this which Wachter (1930), in her classical paper on the molting of the silkworm, calls the "triangle stage."

Next day at some time between 7:30 a.m. and 3 p.m. the skin is actually shed, the actual time tending to differ from species to species (Table I). From the initial appearance of the pale triangle until shortly before the shedding of the skin, the animal remains almost motionless. (Text-fig. 1a). It is, however, still able to walk and gives a perfectly recognizable defensive response if disturbed.

For about half an hour before the skin splits, the larva makes numerous small contortions within the old skin. The skin appears shrivelled and the scoli along thorax and abdomen are moved independantly of each other, due presumably to local contractions inside the larva as the muscle attachments are being freed from the old cuticle. This activity may continue for about ten minutes. The head is then bent gradually back so that the old capsule is at right angles to the long axis of the body (Text-fig. 1b). The cuticle between the old head capsule and the ventral part of the first thoracic segment spilts and the legs begin to emerge[3]. The whole skin is shifted backward as the larva surges forward and this puts a strain across the dorsal cuticle behind the old capsule. Thus about forty seconds after the third pair of legs has been freed, this connection between the old head capsule and dorsal prothorax breaks and the head is sud-

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[3]Wachter (1930) says that in *Bombyx mori* the bending back of the head occurs because contact between old head capsule and skin is maintained at the mid-dorsal point after being broken ventrally and laterally. This may be true for the Heliconiinae as well.

TEXT-FIG. 1. Diagrammatic representation of four stages during the shedding of the skin of a heliconiid caterpillar. **a**, The pose adopted during the "triangle stage"; **b**, head bent sharply back as the skin begins to tear; **c**, head more extremely bent as the legs emerge; **d**, head jerked down and the caterpillar emerging from the skin which is gathered into folds as it passes back. Newly exposed cuticle is stippled, old head capsule is black and the "triangle" is marked with an arrow.

denly jerked down to its normal position, the old capsule now being stuck loosely onto the mouthparts of the new one. Meanwhile the rest of the old skin is being gradually shifted back by muscular movements which run along the body. In some species, *H. sara, H. ricini* and *D. juno,* which tend to be gregarious, the newly emerged caterpillar puts its feet onto the surface and begins to crawl forward out of its skin, so that waves of movement are assisted by the walking of the larva. There is no strict distinction between these two methods since the behavior is graded from *D. iulia,* in which there is almost no sign of walking forward, to *D. juno* where it is very marked.

Partially correlated with the extent of this walking forward is the degree to which the cast skin is gathered together as a heap or left spread. *D. iulia* and *D. phaetusa* are alone marked in their habit of producing a closely folded mass of exuvium.

The complete shedding of the skin, from the time the head is bent back until the anal prolegs are freed, takes about four minutes. There are, however, slight indications of specific differences in duration (Table II) although these are not consistent enough to evaluate satisfactorily without a larger sample from each species.

Once the skin is freed from the last segment, the hind end is lifted into the air. The anal prolegs contract and expand several times and then the caterpillar begins to rid itself of the old head capsule. This it does by wiping off the capsule against a leaf or stem. As soon as its new capsule is bared, the caterpillar puts its spinneret to the substratum and weaves a small patch of silk just ahead of it. It walks forward a few millimetres and weaves again.

There is a fairly wide variation in the pose adopted during the process of expanding the scoli and spinules of the head and body, but information is too limited to say whether any specific constancy exists among these variations. All species are alike, however, in having head and thorax held away from the substratum. Expansion seems to be effected by periodically rais-

ing the internal pressure of the body and blowing out the scoli and spinules. The contraction which produces this pressure increase is a shortening of the body, the legs being kept free of the ground and the head and thorax pressed back into the abdominal region. During this contraction the arch already present in the thorax may be flattened somewhat towards the substratum, as often happens in *A. vanillae.* The thorax and head may be lifted further and the extent of arching actually increased, an event which is more noticeable in *H. melpomene* and *D. iulia.* The principle effect, a longitudinal shortening of the body, is the same in all species and is often the only one visible. During any one contraction a scolus will expand from the base up and the spinules arising from this expanded portion will "click" into position. Normally it takes about 6-11 contractions to expand a scolus and its spinules fully. There is a very slight tendency for scoli and spinules to collapse again once the pressure which erected them has subsided. A series of 7 contractions lasts approximately 5 minutes, by the end of which time all scoli and spinules are usually fully expanded.

It may be noted that although spine expansion normally begins within a few minutes of the animal's being freed of its skin, disturbance by another caterpillar or other interference may delay its onset for at least 20 minutes without obvious effect upon the form of the spines. Once the expansion is complete, darkening and hardening begin.

The hardening and darkening process occurs gradually and there is no marked activity for 20 to 40 minutes. During this time all species rest with thoracic segments arched, legs somewhat spread and head slightly bowed. *D. iulia* and *H. aliphera* frequently adopt a "J" position as well, the head and thorax between O° and 90° to the rest of the body in both dorso-ventral and lateral planes. The caterpillar then relaxes so that its legs touch the leaf or stem again, but it may remain motionless for another one to four hours. It then turns slowly round, may rest again but finally walks back to its empty skin and begins to eat it.

TABLE II. EXAMPLES OF RECORDS OF BEHAVIOR DURING SHEDDING OF LARVAL SKIN BY SPECIES OF HELICONIINE CATERPILLARS

Species	Duration of the shedding of the skin (mins., secs.)	Duration of spine expansion (mins., secs.)	Number of contractions in spine expansion
Dione juno	5,15	?	?
	5,00	?	?
	4,00	5, 20	7
	23,40	5, 00	5
	5,00	4, 10	5
	6,00	?	?
Agraulis vanillae	4,40	?	?
	4,45	6, 10	6
	3,10	5, 40	6
	5,35	6, 20	10
Dryas iulia	3,20	?	?
	2,20	6, 20	9
	2,30	4, 35	8
	?	5, 20	9
	2,45	8, 20	11
Dryadula phaetusa	3,20	5, 30	5
	?	4, 00	+3
Heliconius aliphera	?	10, 15	11
	2,30	?	?
	2,30	7, 45	7
Heliconius melpomene	3,40	10, 55	8
	3,30	5, 10-6, 50	11
	3,05	6, 50	5
	2,50	4, 55	7
Heliconius erato	5,00	3, 25-7, 25	?
Heliconius ricini	3,05	6, 15	2
Heliconius sara	3,20	6, 00	?
	3,30	7, 00	2, indistinct
	2,10+	3, 00+	?

In *D. iulia* and *D. phaetusa*, but not in other species, there is a great deal of arching of both head and hind end during the period between the end of hardening and eating the skin. The legs and anal and last abdominal prolegs are freed and arched up so that the hind end and head almost meet above the caterpillar's body.

If there happens to be the cast skin of another caterpillar immediately in front of a larva which has just finished its hardening and darkening, it will not turn round and go back to eat its own skin but will walk forward and accept the foreign one. This indicates that the behavioral sequence leading to the eating of exuvia is not strictly stereotyped. After the skin has been eaten there is a further period of rest before the caterpillar begins to feed on a leaf. If, however, a second skin is offered to a newly molted caterpillar it will eat this as well, a phenomenon often

seen to occur naturally among gregarious species such as *H. sara*. Thus eating a single empty skin does not, in itself, provide the whole consummatory act.

D. juno and *H. sara*, two of the gregarious species, differ from *A. vanillae, D. iulia, D. phaetusa, H. aliphera, H. isabella, H. melpomene, H. erato* and to a lesser extent *H. ricini* in the appearance of the spine expansion process. Instead of being a definite series of clear-cut contractions, there is an indistinct period during which the scoli gradually expand. While this could be a genuine effect, it seems more likely that it is due to the observational set-up. The gregarious species have shorter scoli and less developed spination (Beebe, Crane & Fleming, 1960). Thus they provide less distinct indicators of the process which is being observed than would caterpillars of solitary species. In addition,

TABLE III. PREPUPATIONAL BEHAVIOR IN SPECIES OF HELICONIINE CATERPILLARS

Data on *Dione juno* relate to a single group of 13 larvae observed in this study but are confirmed by the record of another group kept by Constance Carter. *Dryadula phaetusa* record refers to a single animal. Information relating to *Heliconius sara* supplied by Constance Carter.

Species	Approx. duration of fast before site select. (hours)	Locomotion during site select., mins./meter	Normal time of day for:		
			Site select.	Hanging up	Shedding last larval skin
Dione juno	8	1,44–3,04	8:30 p.m.	11:00 p.m.	1:00-4:00 p.m.
Agraulis vanillae	6-14	2,22–7,59	Indistinct	5:00 p.m.	7:00-11:30 a.m.
Dryadula phaetusa	4	10,12	3:00 p.m.	5:00 p.m.	Before noon
Dryas iulia	5	1,24–1,58	2:30 p.m.	5:00-8:00 p.m.	8:00 a.m.-noon
Heliconius isabella	0	2,05–3,43	2:30 p.m.	3:00-7:00 p.m.	?
Heliconius aliphera	0	–5,30	2:00 p.m.	3:00-7:00 p.m.	9:30-noon
Heliconius melpomene	1-8	2,55–3,16	11:00 a.m.-1:30 p.m.	1:30-7:00 p.m.	7:00-11:30 a.m.
Heliconius erato	1	3,18–4,25	9:30 a.m.-12:30 p.m.	12:30-3:00 p.m.	8:00-10:30 a.m.
Heliconius ricini	¼-1	3,20–4,50	10:30 a.m.-1:30 p.m.	1:00-5:00 p.m.	7:30-9:30 a.m.
Heliconius sara	?	3,14–	10:30 a.m.	5:00 p.m.	?

the caterpillars are together in a group and more difficult to distinguish individually. Moreover they are frequently moving and disturbing each other.

III. PUPATION

a. *Selection of Pupational Site*

As can be seen from Table III, most species stop feeding some hours before they start to find a site suitable for pupation. There are no noticeable behavioral changes during this period but changes take place in the coloration (Beebe, Crane & Fleming, 1960). The caterpillar rests either on the leaf it had been eating or on the stem.

Once they have begun to search for a pupation site, the caterpillars no longer feed. *H. isabella* is exceptional for it may sometimes stop and eat again even after it has abandoned a feeding position and begun the ambulatory phase. None of the species which pupate on leaves has ever been seen to do so on a leaf which has already been chewed by a caterpillar or one on which another larva is resting.

Some indication of the speed with which caterpillars of different species walk is given in Table III. (This has not been corrected for the slightly different temperatures at which the observations were made.) Only *D. iulia* is exceptional in walking invariably fast. *D. phaetusa* is odd in being very slow but as only one individual was tested, no valid conclusions can be drawn from this. The rate of walking varies during the ambulatory phase, starting slowly, increasing, then apparently falling again—an effect which partially accounts for the wide variation in results presented here. Except in the cases of *A. vanillae*, *D. phaetusa* and *H. erato*, the walk is interrupted by few rests. A caterpillar may drop from one part of the vine to another or to the ground, covering a small area of its leaf or stem with silk and then swinging down from this on a safety thread. Sometimes the drop may be as much as a meter.

Once a caterpillar has started walking, it may pass numbers of what appear to be suitable pupation sites, a behavioral feature noted in the cecropia silkworm (v.d. Kloot & Williams, 1953). It should be noted, however, that at least some *D. iulia* and *H. melpomene* are able to settle at a pupation site after walking only a few inches. The location of such a site differs from species to species, as can be seen in Table IV, yet it is always such that the pupa can hang

TABLE IV. SITES SELECTED FOR PUPATION BY PREPUPATIONAL HELICONIINE CATERPILLARS HAVING
FAIRLY UNRESTRICTED CHOICE
L=Living, D=Dead in reference to stem and tendril.

Species	Leaf tip	Leaf blade	Pet-iole	Midrib	Leaf margin	Stem, L., D.	Tendril
Dione juno	—	—	—	—	—	3L	10L
Agraulis vanillae	—	—	—	2	—	6L	1
Dryadula phaetusa	—	—	—	—	—	1L	—
Dryas iulia	—	1	3	2	—	2L & 12D	5
Heliconius isabella	—	12	—	—	—	—	—
Heliconius aliphera	—	4	—	12	—	—	—
Heliconius melpomene	—	—	—	10	3	—	2
Heliconius erato	2	—	—	1	1	2L	2
Heliconius ricini	—	—	—	10	3	1L	5
Heliconius sara	—	—	—	2	—	1	—

down below it, whether it be beneath a leaf, stem, tendril, flower stalk or some foreign horizontal surface. Occasionally a caterpillar may attach against a vertical surface.

One feature which normally determines if a site is suitable, is whether it provides enough free space beneath for the pupa. This is estimated by means of a behavior pattern which will be termed "trying for height." Taking *H. melpomene* as an example, the caterpillar walks along the ventral midrib of a fresh, unchewed leaf as it goes weaving on either side of the midrib. Towards the center of the leaf it stops and weaves more actively. Then it arches its head back and releases its foothold so that its head and thorax hang loose beneath the leaf. If it touches a second leaf or some other object below, it will usually abandon the position as a possible pupation site. If it does not touch anything, it releases the hold of its first and then second prolegs so that its body hangs further down beneath the leaf. It may swing gently, reaching out around it. If it now touches some object, the caterpillar does not grasp it and crawl onto it as it would if it were trying to move away, but will usually contract up onto the midrib again and walk off to try another leaf. A caterpillar usually tries for height three or four times, facing first one way along the midrib and then another. Finally, if the leaf is acceptable,

it will rest before beginning to spin its pupal silk pad.

H. aliphera and *H. isabella* differ from the other species in that, when trying for height, the prolegs are never freed from the leaf above. In these two species the pupae do not hang directly but are bent almost at right angles to their support (Plate I). They therefore need less space beneath their pupation site.

Other immediate features which render a site desirable for pupation are less clear. Field observations show that all species except *H. isabella*, and to a more limited extent *H. aliphera*, choose to hang up on a ridge, a knob or other protuberance or irregularity, never on a smooth surface. In the laboratory *H. isabella*, given the choice of an irregular surface, such as aluminum gauze, or a smooth one such as glass, will hang up on the latter. The same preference is also shown by *H. aliphera* (Plate I), which in the field pupated on the ventral midribs of leaves in 12 out of 16 cases. Those four which were not on midribs were, nevertheless, in positions which would have been acceptable to *H. isabella*.

In broader terms a pupation site must, so far as possible, protect the pupa and permit a healthy butterfly to emerge. Protection against climatic factors is unlikely to be important, in that the pupae are in an environment which already supports the caterpillars. Nothing at all is known

of pupal predators, although ants will attack pupae which are injured or unhealthy; they have not been seen to molest them otherwise. Various insect parasites, both dipteran and hymenopteran, can be bred out of pupae and it has been established that the eggs of one of these are laid by the female in the pupa itself. What does seem to be a significant hazard, however, is that another caterpillar, of the same or a different species, will begin to eat away the leaf from around a pupa so that the pupa falls to the ground. This has happened at least four times on the observational vines when there have been plenty of other leaves available for the larvae. Some of the consequences of a pupa falling to the ground will be considered later.

Meaningful discussion of the significance of a preferred pupation site, and consequently of the prepupational behavior of the caterpillar, must necessarily be unsatisfactory until more exact information is available about potential pupal predators and parasites. Those species which hatitually move off their leaves to pupate (e. g., *D. iulia*). risk attack by predators such as ants or mantids (and both have been observed to kill caterpillars searching for pupational sites) during this extended locomotory stage. There may be compensation for such dangers in their subsequent security from being chewed off a leaf.

b. *Pupational Behavior*

Once the site has been chosen, the caterpillar weaves generally around it and may tie the selected structure firmly onto the main vine. Then it spins silk more particularly in the region where the pupal pad is to be placed. There are several rest periods during which, if oriented under a leaf or along a stem, the caterpillar faces first one way, then the other. Eventually, after 30 minutes to two hours, spinning of the pad itself begins. The caterpillar first spins on one side of the midrib, stem or tendril, then, bringing its spinneret to the place where the pad is to be, touches the spot, lifts its head and pulls it backwards, touches the spinneret again to the position of the pad and then repeats the procedure, but turning this time to the other side. The process is repeated many times before the spinning becomes concentrated on the pad itself. The drawing back of the head over the area where the pad is being spun is concerned with forming loops of silk which make up much of the pad and has been discussed in Part I of this paper as "yawning." The pad is cone-shaped with an elliptical base whose long axis is about 1 mm. long. It is about 0.5 mm. tall and its apex is asymmetrically placed, being nearer to the caterpillar as it spins than the mid-point of the base. The color of the silk varies from species to species (Table V).

Once the pad is completed, the caterpillar moves forward until the pad is either just before or behind its fourth pair of prolegs. In this position the animal waits until it has emptied its gut of the last fecal pellet. Then it walks further forward so that its anal prolegs touch the pad. These structures work themselves into the silk,

TABLE V. COLORS OF SILK WHICH HELICONIINE
PREPUPATIONAL LARVAE PRODUCED IN SPINNING THEIR PUPAL PADS

Species	White	Pale pink	Pink	Red	Indeterminate
Dione					
juno	13	—	—	—	—
Agraulis					
vanillae	9	—	—	—	—
Dryadula					
phaetusa	2	—	—	—	—
Dryas iulia	21	—	—	—	—
Heliconius					
isabella	9	—	—	—	—
Heliconius					
aliphera	11	—	—	—	—
Heliconius					
melpomene	—	1	—	12	2
Heliconius					
erato	—	2	2	—	2
Heliconius					
ricini	1	3	8	—	3
Heliconius					
sara	5	—	—	—	—

presumably much of the attachment being by way of the crochets. The caterpillar jerks its hind end forward and back, either to make the attachment more secure or to test it. Some species immediately loose their hold on the leaf or stem and hang freely from the pad, *e. g. D. iulia* and *H. melpomene*. Others such as *A. vanillae* may wait for as long as half an hour. When the prolegs release their hold on the substratum, it is the hindermost abdominal pair which let go first, then the third prolegs and finally the second and first. The caterpillar rests in this position until the following morning, when it sheds its skin.

If the observer pokes a larva which has just released its foothold and is hanging by its anal prolegs, it can be induced to climb back onto the leaf or stem. If the disturbance is rough enough, the caterpillar will break its attachment to the silk pad. It may then rest a while before reattaching itself once more to the original pad or may spin a second one either beside the first or a short distance off. There is no need for the caterpillar to revert to the previous locomotory stage before it can spin a second pad, in the way that cecropia larvae seem constrained to do if removed from a partly constructed cocoon (v. d. Kloot & Williams, 1953).

D. iulia and *H. melpomene* can be induced

by continued teasing to spin a third silk pad, but this is invariably very thin and small. There appear to be differences in the ease with which different species can be teased into abandoning their pads or spinning a second. Thus *A. vanillae* is markedly reluctant to climb back onto the substratum and will twist and try to bite at the teasing forceps for much longer than would *H. melpomene*. No standards were established for the teasing, however, and a great deal more experimentation is necessary before evaluating any such specific differences.

A peculiar point emerging from these latter observations is that the pattern of hanging free after attachment to the pad changes with repetition. On the first occasion it is invariably the hinder of the prolegs which loose their hold first. On the second attempt the prolegs hang free in order from the front to the back. The possible interest attaching to the point is that it suggests that the second hanging-up is not in all ways a simple repetition of the first.

IV. Pupal Behavior and Adaptations

Of the ten species of heliconiine pupae which have been observed, all show a certain amount of movement. This is distinct from any flexibility which they may have at the point of attachment. This latter characteristic differs from species to

TABLE VI. Behavioral and Pigmentary Characteristics of Heliconiine Pupae

Information relating to *Heliconius sara* supplied by Constance Carter; details of methods of measuring flexibility not strictly comparable with those of other species. Position of *H. sara* in the series is therefore open to suspicion.

| Species	Degree of flexibility	Bend in pupa	Odor production	Stridulation	Gold spots
Heliconius isabella	160	Permanent	−	+	−
Heliconius aliphera	160	Permanent	−	+	−
Agraulis vanillae	147	Changing	−	+	−
(*Heliconius sara*)	(144)	−	?	?	+
Dione juno	136	Changing	−	+	−
Dryas iulia	126	−	+ +	+ +	+
Dryadula phaetusa	125	−	−	−	+ +
Heliconius ricini	116	−	+	+	+ +
Heliconius melpomene	79	−	+ +	+ +	+ +
Heliconius erato	65	−	+	+	+ +

species, presumably depending on how tightly the pupa has attached its cremaster to the silk pad. Flexibility may be expressed by how far the pupa rotates while its support is rotated through 180° in the vertical plane. An absolutely rigid attachment gives the full 180° turn while a fully flexible pupa will not rotate at all. In this way, the ten species available for testing can be arranged in a series (Table VI).

Hinton (1955) discusses the selective advantage derived by such pensile pupae from their flexibility of attachment, contending that swinging hinders predators such as birds from getting an effective peck or that is it useful in shaking off ants. Whether such factors are involved among the heliconiine pupae or not, flexibility certainly adds to the effect of the movement of the pupa itself.

When the species of Heliconiinae studied are arranged according to other aspects of pupal behavior, the series established for flexibility of attachment tends to be repeated. Thus in the two species which are rigidly attached, *H. isabella* and *H. aliphera,* the posterior segments of the abdomen are bent so that the ventral surface lies near or touches the surface of the leaf and the angle between body and leaf is invariably less then 35°. The pupae of these species are the least active of all those studied. When touched by caterpillars or the experimenter, they swing from side to side but produce only faintly audible stridulation. Both are light colored, creamy white or translucent (with a suggestion of green in *H. aliphera*). Their markings are faint brownish or black without gold spots or other "attention calling" devices. Neither produces any perceptible odor. Considered as a whole, the behavior and appearance of the pupae of these two species suggest that the evolutionary trend in the pupal stages of *H. aliphera* and *H. isabella* has been towards camouflage and concealment rather than advertisement.

The next two pupae on the flexibility scale, *A. vanillae* and *D. juno,* share with *H. aliphera* and *H. isabella* the characteristic of bending their bodies so that they do not hang vertically down as do the other five species. They do not, however, bend up close to the support nor do they remain in this position until emergence. The major bend in the body of the pupa is more characteristically lateral as opposed to the dorso-ventral one in *H. aliphera* and *H. isabella;* further, *A. vanillae* and *D. juno* frequently have two distinct bends, one almost at right angles to the other (Text-fig. 2). During the nine or ten days of pupal life the orientation of these bends constantly changes; without any apparent environmental stimulus a pupa will twist its body into a new position. A few hours before emergence of the adult, they straighten out so that the pupa hangs vertically down. This again is distinct from the behavior of *H. aliphera* and *H. isabella,* whose adults emerge from a pupa which is still curved upwards towards the leaf. It may be noticed that, for the butterfly to expand its
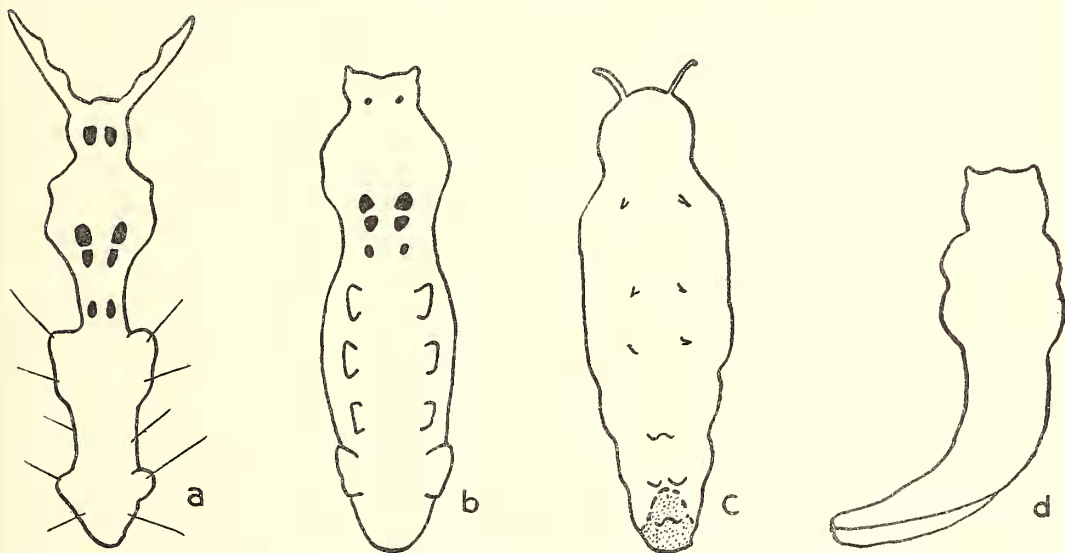
TEXT-FIG 2 . Diagrammatic representation of the main morphological and some behavioral characteristics of the pupae discussed in the text. Dorsal view of: **a**, *H. erato;* **b**, *D. iulia;* **c**, *H. aliphera;* **d**, *A. vanillae.* Gold markings are shown in solid black and the ventral bend in the posterior end of *H. aliphera* is indicated by stippling.

wings, a free space is needed beneath the empty pupal case to which it clings. Since the pupae of *H. aliphera* and *H. isabella* remain bent during emergence, less space is required than when the pupae straighten out as do those of *D. juno* and *A. vanillae*. It will be remembered in this connection that *H. aliphera* and *H. isabella* do not release their prolegs when "trying for height" (see page 110) while *D. juno* and *A. vanillae* usually do.

The pupae of *D. juno* and *A. vanillae* make no audible sound when stimulated, nor do they produce any noticeable odor. Their movement is slight, rather slow and limited. They have no bright spots or grotesque frills or spines and their usual colors are neutral straw to brown-gray (Beebe, Crane & Fleming, 1960). *A. vanillae* pupates on fresh vine, either on the stem, tendrils, flowers or leaves, and almost invariably on its own food-plant. The brownish color combines with the bendings of the body to give the pupa a resemblance to a shrivelled leaf or withered flower of *P. foetida*. Like *A. aliphera* and *H. isabella*, the pupae of this species seem to be adapted rather toward concealment than warning or frightening away possible predators.

Of a group of 13 healthy *D. juno* caterpillars given a choice of pupational sites, all hung up on the stem, tendrils or leaves of a fresh vine. Although they resembled *A. vanillae* in their choice of a pupation site, they remained together as a group and it is hard to see any attempt at concealment in their behavior.

The fact that both *D. juno* and *A. vanillae* continually change from one twisted position to another during the pupal stage is interesting when compared with the constant bend of the abdomen of *H. aliphera* and *H. isabella*. The latter two are flexed directly back, *i. e.*, their bend is a bilaterally symmetrical one. It seems likely that if a pupa is asymmetrically twisted throughout its entire pupal life, the development of a bilaterally symmetrical butterfly would be more difficult. Thus a pupa of *D. iulia* which had been put onto a flat surface immediately after it had molted, and was still soft, hardened with a permanent twist to one side. When the butterfly emerged, the wing on the concave side was shorter than the other and buckled; the animal was barely able to flutter. Thus it may be advantageous for a pupa to remain bilaterally symmetrical. Since shrivelled leaves are seldom so, *A. vanillae* (perhaps *D. juno* as well) has to lose its symmetry to mimic such objects. Possibly the continual changing of the asymmetrical pose is a compensatory measure which ensures that the developing adult is not continuously exposed to a single pattern of asymmetric forces.

The pupae of the five remaining species hang vertically and are fairly flexible. With the exception of *D. phaetusa* (of which only one specimen was tested), they all wiggle suddenly and furiously when stimulated. Again with the exception of *D. phaetusa*, they produce a clearly audible squeaking. All except *D. phaetusa* produce a sudden and noticeable smell when disturbed. *H. melpomene* smells most strongly, an odor very like that produced by the adult butterfly when disturbed. This is unpleasant to some people, not to others — it passes very quickly. The pupae of *D. iulia* smell of musty honey, those of *H. ricini* and *H. erato* have a weaker odor somewhat like a mixture of *D. iulia* and *H. melpomene*. There are in addition bizarre anatomical effects (Beebe, Crane & Fleming, 1960). All five species, *D. phaetusa* included, have showy golden or silver spots on their backs (Text-fig. 2). *H. melpomene* is chestnut colored with black spines and is fairly obvious against the green of the leaves under which it normally pupates. *H. ricini* and *H. erato* have elaborate antler-like frontal horns, protuberances and spines on their bodies.

All these features, behavioral and structural, seem to advertise the pupae, and are thus the converse of the tendency shown in *H. aliphera*, *H. isabella*, *D. juno* and *A. vanillae*. However the site in which *D. iulia* chooses to pupate, up against the bark of a tree or on a shrivelled tendril or flower, combines with the mottled appearance of the animal to make it almost invisible in its natural position. The gold spots, so obvious in *H. melopene* and especially *D. phaetusa*, are in *D. iulia* very much smaller and the most anterior pair are almost invisible. In *D. iulia* and probably also *A. vanillae*, there is a tendency for the shade of the pupa to be influenced by the lighting conditions under which the larva hung up, a tendency well known among lepidopterous larvae and first investigated by Poulton as early as 1887. If *D. iulia* is kept in the dark during the day on which is it due to hang up, the resultant pupa is much darker than one kept in the light[4]. In these features therefore the pupa of *D. iulia* appears to be cryptic. In this case selection may be working in these two directions at once, and they do not necessarily cancel each other out nor are they mutually exclusive. A pupa which is concealed may be discovered accidentally by a predator and it would then be advantageous for it to have an intimidation display. If an "advertisement policy" like that of *H. mel-*

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[4]Although this experiment was carried out in a single room with only a partition separating "light" from "dark" larvae, there is no guarantee that some temperature difference did not exist.

pomene were modified so as to retain only those elements such as noise, movement or odor, which the pupa can control, then a condition like that in *D. iulia* would result. Perhaps the turning point in such an evolutionary pathway would be that of changing the pupational site from beneath a leaf to a stem, tendril or foreign surface. This change in its turn could have resulted from selection pressure of caterpillars eating the sheltering leaves or from the fact that leaves on the particular species of vine are scarce or very flexible—both of the latter tend to be true in the case of *P. tuberosa*, the vine on which *D. iulia* feeds.

H. ricini and *H. erato* are usually cryptically placed, but less so than *D. iulia* (Table IV). About half of the cases observed were not on living leaves. The explanation suggested for *D. iulia* can be put forward for these two species as well, although with perhaps less justification.

The case of *D. phaetusa* is not explicable in such terms. The only feature which could be regarded as intimidating is the spotting. It has no marked movement, sound or smell. On the other hand, the pupa does not appear to be well concealed, being light beige without striking peculiarities of any sort. Perhaps some simple adaptive explanation will be revealed by observations in the field.

V. Emergence from the Pupa

The duration of the pupal stage in the Heliconiinae is generally 9 or 10 days. There is a suggestion of some specific differences in what time of day emergence takes place; thus *H. erato* is usually out of its pupal case before 9 a.m., while *H. melpomene* tends to come out throughout the morning, with a concentration around 10:30 a.m.

The pupal case cracks across behind the head, down the center of the thoracic tergites, then across and down either side of the wing covers. The lateral edges of the split behind the head run down onto the ventral surface of the pupal case and along the ventral edges of the wing covers. Thus the thoracic part of the pupal case is divided longitudinally into three sections which can be easily separated from each other and from which the wings and legs of the butterfly can emerge without excess straining. The separation of the three sectors seems to be effected mainly by movements of the bases of the wings, which, expanding and contracting against the loose sections, gradually work them apart. Presumably in its normal hanging position this would be helped by gravity as the body tends to fall out of the pupal case. The legs do, however, grasp feebly at the edges of the case and within a few seconds either by their effort, by waves of movement passing back or by gravity, the swollen abdomen is freed of the case. The butterfly immediately turns around so that the small wing buds, antennae and abdomen hang down behind it.

The wings at this time are about one-third of their final length and during the next two to five minutes they expand until they reach full length. When fully expanded, the wings are almost completely flattened. Although they are soft and flaccid to the touch, they do not fall into folds as an equally soft cloth would do. The antennae hang straight back, lying between the wings. The labial palps have moved from their original position, folded down into the thorax, to their final one, bent up beside the compound eyes.

At intervals for a period of 15 to 30 minutes the wings flap slightly open and then close again, the intervals between the opening and closing depending to some extent on the species, examples of which are shown in Text-fig. 3. During these movements the two wings of each side are held together with the hind wing a little further forward relative to the front than is normally the case. As the wings open, the head moves slightly forward and the abdomen swings between them. When the wings close the head and abdominal movements are reversed. Extension of the proboscis occurs fairly frequently (Text-fig. 3), but without definite relation to the wing movements. The palps begin to tremble a short time after the wing fanning starts and there is a marked tendency for this to be associated with wing closing rather than opening.

At the end of wing fanning, the wings are closed and then the hind ones open again so that they are well separated from the forewings. The latter open only very slightly. The wings are then held motionless in this position for an interval which varies from less than four to more than 15 minutes; the interval will be referred to as the "relaxation period." Depending on the species, the palp trembling will or will not continue throughout the relaxation period (Table VII). The end of relaxation is marked by the hind wings closing up against the forewings. These are, however, still held slightly apart from each other for a further two to four minutes so that the ending is gradual.

A variable time after the start of wing flapping, the antennae move forward to the leading edges of the wings and, when the wings next close, fold back so as to lie lateral to the wings instead of between them. Subsequently

the antennae, together with the head, can be seen to move forward and back as the wings flap. By the beginning of the relaxation period they come to lie together at the leading edge of the wings. During or after relaxation they move anterior to the wings and are held together for a variable time, sometimes opening and closing slightly. In some species, such as *A. vanillae*, this forward movement of the antennae is very characteristic and coincides with the end of palp trembling, though not usually at the end of relaxation.

The first drops of meconium are voided at a time which varies to some extent from species to species (Table VII). The meconium is a brownish, reddish or yellowish fluid, the shade depending on the species of butterfly (Table VIII)[5]. Three to six small drops fall together at

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[5]No attempt has been made to establish whether the color of the meconium is influenced by the vine on which the larva had been feeding. It is surely not the direct cause, in that *H. isabella*, feeding on the same species as *H. melpomene* and *H. ricini*, produces yellow while that of the other two is primarily gray or chestnut. Conversely, *H. melpomene* and *H. erato*, feeding on different vines, produce the same colors. Nor can it be correlated simply with the general pigmentation of the scales.

TEXT-FIG. 3. Examples of records of emergence behavior of *D. juno, A. vanillae, D. phaetusa, D. iulia, H. isabella, H. melpomene, H. ricini* and *H. sara*. The time scale at the top and bottom of the figure is in minutes and zero time for each record is on the left hand side and is the moment when the pupal case split open. The upper saw-toothed line of each record represents activity of the palps, while a continuous line marks periods when inactivity was observed. A vertical stroke indicates wing opening during the period of wing fanning, wing closing being shown by a solid black circle, while a dotted line shows the relaxation period. The open circle with a cross in it marks the liberation of the first drop of meconium. Below this in each record is a representation of the state of the wings, starting with a pair of wavy lines at the left of each record and representing the crumpled wings at the last point of time when they were mentioned in the laboratory notes as being crumpled prior to the straightening, which is represented by straight lines. The position of the antennal tips is shown relative to the wings as pairs of black dots.

TABLE VII. BEHAVIOR OF EMERGENT HELICONIINE BUTTERFLIES

Number in [ ] after each species denotes number of cases watched in detail; number followed by an "e" indicates additional cases of experimental animals. (See Table IX).

Species	Number of flaps and number of minutes of phase	Number of flaps per minute	Palp movement obvious during flapping	Palp movement obvious during relaxation period	Minutes before 1st meconium shed. Co-efficient of variation (bracketed)	Final palp movement and head twisting
Dione juno [8]	14/16–18/17	1.0	+	+	20.7 (.07)	+++
Agraulis vanillae [5] [2e]	10/9.0–17/10	1.3	Absent or late	+	29.6 (.06)	+++
Dryadula phaetusa [1]	32/23	1.4	++		32.0 (?)	++
Dryas iulia [6] [9e]	18/13–24/13	1.6	++		17.8 (.21)	+++
Heliconius isabella [3] [1e]	26/17–28/16	1.6	++ late	+	32.0 (.03)	–
Heliconius aliphera [2]	21/16–29/19	1.55	–	–	21.5	–
Heliconius melpomene [8] [2e]	19/15–27/17	1.4	+++ (on shut)	–	10.8 (.45)	–
Heliconius erato [1] [3e]	22/15	1.4	+ (on shut)	–	23.1 (.58)	–
Heliconius ricini [4] [2e]	21/14–25/15	1.5	+ (on shut)	–	21.3 (.16)	–
Heliconius sara [2]	22/10	2.1	+++ (on shut)	–	13.7 (.10)	–

intervals of a few minutes until the animal is ready to fly. The first two or three sets of drops contain a fine precipitate but later drops become more transparent and paler in color until after a period varying from 6 to 40 minutes the fluid is altogether clear.

Once the relaxation period is over and the wings are once more apposed, only slight movements of the antennae take place before the animal flies off. They do, however, gradually move further and further apart until their normal position is achieved. Just before flight a peculiar pattern has been noticed in *D. juno, A. vanillae, D. phaetusa* and *D. iulia*. The butterfly twists its head from one side to the other, at the same time extending and waggling its palps, one after the other.

Flight takes place after the antennae are well apart, although a disturbance before this time may cause the butterfly to flap its wings. The stimulus for flight often comes from the movement of a nearby butterfly or a puff of wind but frequently there is no apparent external stimulus at all. The insect walks up its empty pupal case, flapping its wings, then suddenly takes off, sometimes still dropping meconium as it flies.

The specific differences among the 10 species

observed are listed in Table VII and some can be seen in Text-fig. 3.

During a natural emergence there is very little rearrangement of the legs and body necessary before the butterfly is in the position appropriate for wing fanning. The preferred position is one in which the longitudinal axis of the thorax is not quite horizontal, sloping slightly upward at the anterior end. In the majority of species examined, the pupae have projections on the dorsal part of abdominal segments and these are placed so that the newly emerged butterfly can obtain its preferred pose by clinging onto them with the first pair of functional legs and onto the margin of the head case with the others. However, the stance does not invariably occur and it may not be correct to regard such projections as having been evolved primarily for this function.

Emergence from the pupal case is almost invariably prolonged when the animal is not hanging in the normal way. If, however, an object is placed near the butterfly's legs as soon as these are free, it is grasped and the body and wings pulled out quite quickly.

If a recently emerged butterfly is not provided with an appropriate resting place, it walks until it finds one and, in *H. melpomene* at least, is

capable of searching for at least 27 minutes. Its walking is initially directed toward the lightest part of the horizon but this orientation gradually becomes confused and the butterfly tends to begin circling movements, possibly due to mechanical difficulties with its wings.

During this walking stage the inflation of the wings is not delayed and within five minutes of its exit from the pupal case the animal's wings are fully expanded and flattened. If the butterfly is allowed to hang up at this stage, it shows no apparent deviation from the normal pattern of wing flapping, palp trembling, relaxation and finally flight. Yet even when it is forced to walk on a flat surface there may be some damage to the wings, either from scraping on the pupal case or injury during walking. There may also be a fair amount of bleeding from both wings, although the effects are not as serious as Brocher (1919) reported for punctures made at an earlier stage in the wings of Agrionidae where full expansion was prevented. In natural conditions, after a pupa has fallen to the ground as a result of the chewing activity of some other caterpillar, its newly emerged butterfly may have to walk over twigs, leaves or other debris and will probably damage its wings more severely.

If the butterfly is forced to continue walking after the wing expansion is completed, the wings trail limply behind it and during this time there are no signs of any flapping behavior, nor are the palps trembled at all. Meconium will nevertheless be dropped at the appropriate time. When eventually the butterfly is allowed to hang up, the wing flapping may be prolonged, or much curtailed; it may be much faster, or just irregular (Table IX). If the butterfly is forced to walk for as long as 10 minutes, its wings, when eventually it does hang up, fall into folds instead of remaining flattened. Although they appear still to be soft, the animal seems unable to hold them in such a way that they harden as flat surfaces. Thus, although they are fully expanded, the ability to flatten the wings seems to disappear about eight minutes after emergence from the pupal case. Normal wing expansion may sometimes take as long as five minutes, so the flattening process cannot be postponed for more than about three minutes after its normal time. Hardening of the wings must occur very shortly after the loss of flattening ability, for when hanging up is delayed for longer than eight minutes, the wings begin to take on the shape they had when trailing along behind the walking butterfly. If they were twisted over the right side, the hardened wings later show the same twist. Indeed, it is likely that straightening and hardening normally take place concurrently.

Even if its wings have hardened in a distorted and useless condition, the butterfly, after a period of some wing flapping and violent palp trembling, relaxes for a period, rests and then finally tries to fly. Although the wings may be so twisted that their pattern is unrecognizable, the butterfly still rests for the normal relaxation period and then attempts to flap the wings prior to take off.

Like the wings, the antennae may remain unstraightened unless they are allowed to hang straight back between the wings. The critical period for this event appears to be the same as that for wing flattening and hardening.

Wing flapping and palp trembling are definitely not concerned with wing expansion. They normally occur during the process of flattening and hardening the wings and are curtailed when enforced walking is continued so long that the wings are never correctly flattened and hardened. It thus seems likely that these behavioral activi-

TABLE VIII. COLORS OF FIRST MECONIUM PRODUCED BY EMERGENT HELICONIINE BUTTERFLIES

| Species | Brown | Chestnut | | Yellow | Gray |
		Dark	Light		
Dione juno	4	4	1	—	—
Agraulis vanillae	—	5	—	—	—
Dryadula phaetusa	—	—	1	—	—
Dryas iulia	2	5	6	—	—
Heliconius isabella	—	—	—	4	—
Heliconius aliphera	—	—	—	3	—
Heliconius melpomene	2 (+ red)	1 (+ red)	—	—	15
Heliconius erato	—	—	—	—	5
Heliconius ricini	—	4 (+ red)	3	—	—
Heliconius sara	—	—	—	—	3

ties are concerned in some manner with processes associated with hardening.

In relation to survival the important point is that if within eight minutes of emerging from its pupal case an adult can reach a position suitable for flattening and hardening of its wings, no harm should result if it had fallen or been chewed from its natural support. It must however be recognized that a pupa lying on the ground may well be more susceptible to attack by ants or small mammals or to destruction by molds. Thus the critical significance of selection of pupation sites, in relation to being chewed free by other larvae, cannot be dismissed yet.

VI. Phylogenetic Discussion

Similarities and differences between the larval behavior of some of the species of the Heliconiinae became apparent in Part I of this paper and phylogenetic considerations dependent on them have already been briefly dealt with. Part II provides more material and, in addition, features of the pupae and behavior patterns of the emerging imago. As in Part I, attempts have been made throughout the description to explain the presence of these in terms of the factors which control their appearance and of their possible selective advantage to the species. It is necessary now to see how far these latter behavioral characteristics may be of phylogenetic importance.

Considering the phylogenetic age of the molting patterns and the improbability that they are strongly influenced by the food plant of the caterpillar, it is in fact surprising that there are any specific differences here at all. Yet the position taken up on the vine prior to molting is specifically determined to a large extent and can be partially correlated with feeding and resting positions (Part I). Those species, *H. erato, D. iulia* and *A. vanillae,* which tend to rest on the stem, frequently molt there as well—in contrast to *H. aliphera, H. melpomene, H. isabella* and to a lesser extent *H. ricini.* It is noticeable that *H. aliphera* is more like the other species of *Heliconius* in molting under the midrib of a leaf than is *H. isabella,* which molts on the blade of the leaf. This intermediate position of *H. aliphera* was evident in the consideration of feeding of the larvae and will be remarked later in relation to behavior of pupae and emergent butterflies.

TABLE IX. Examples of Records of Fanning Behavior in Emergent Butterflies under Normal Conditions and when Forced to Walk for Various Lengths of Time after Emerging from Pupal Case

| Species | Number of wing beats during wing fanning, given in minutes and seconds: | |
	Normal conditions	Butterfly forced to walk for number mins. shown in parentheses
Agraulis vanillae	17 in 10 13 " 10 11 " 10 11 " 9 10 " 9	? in 9, 30 (15)
Dryas iulia	24 in 13 21 " 13 18 " 13	18 in 10, 30 (6) 17 " 10 (5½) 15 " 7 (12)
Heliconius isabella	26 in 17 25 " 17 28 " 16 +22 " +13	23 in 15 (7)
Heliconius melpomene	27 in 17 22 " 17 20 " 15 19 " 15 ? " 15 22 " 14	31 in 22 (6) 20 " 10, 50 (2¼)
Heliconius erato	22 in 15	24 in 13, 10 (12) 12 " 11 (7½)
Heliconius ricini	22 in 17 25 " 15 21 " 14	21 in 11, 15 (8) 16 " 10, 35 (6½)

Gregarious species, *D. juno, H. sara* and, less markedly, *H. ricini,* molt together on a stem although in normal resting they are often found on the leaf they had been eating.

Likewise the pose adopted prior to molting is related to that usually taken by a resting caterpillar and is thus species-specific to some extent.

There is less variation between the species when it comes to the actual shedding of the skin and subsequent expansion of the scoli and spines. There is but a slight suggestion that *A. vanillae* waits longer during the triangle stage than do the others and that *H. sara, H. ricini, H. erato, H. melpomene, H. aliphera* and *D. juno* are towards the other extreme in a short wait. Once the caterpillar does begin shedding its skin, the process is almost invariably slower in *A. vanillae* than other species, a feature which might well appear among caterpillars which are relatively unspecialized or unlikely to be interrupted by others during the molting process. Conversely the habit of shedding empty head capsules before the skin is free is one which might be retained in an unspecialized species or acquired as part of the plasticity necessary when gregarious caterpillars are molting together. It occurs in *A. vanillae, D. juno, H. ricini* and *H. sara.*

D. iulia and *D. phaetusa* were seen in Part I to share many behavioral characteristics of feeding and resting. Both show two peculiarities in molting behavior—leaving the cast skin in a small heap instead of spreading it out as they emerge from it, and the marked head-to-tail arching after spine expansion.

There are quite marked differences in the choice of pupation site and these can be correlated to some extent with specific differences in feeding, resting and weaving behavior. In feeding both *H. aliphera* and more noticeably *H. isabella* orient on the blade of a leaf. Resting always takes place on the blade and molting has not been seen to occur anywhere other than on a leaf blade in these two species. The emphasis on weaving has already been mentioned in *H. aliphera* and *H. isabella* and its possible correlation with larval life spent primarily on a smooth blade. Selection of a pupation site can be seen as part of the same syndrome: fifth instar *H. isabella* caterpillars invariably hang up on the ventral surface of a leaf blade if possible while those of *H. aliphera* show definite indications of the same tendency. *H. isabella* is in many other characteristics more specialized than *H. aliphera* and these two species are alone among the Trinidad heliconiines in their choice of pupation site. Thus it seems justifiable to assume that the choice of the smooth surface of a leaf blade as a pupation site is a specialization among them.

Among the species studied, *D. iulia* is unique in its rapid and almost invariably long journey to find a pupation site on a foreign plant or surface. On the other hand, it is the most catholic in its final choice—a characteristic which is seldom associated with specialization. *D. phaetusa,* which in respect of feeding, resting and molting is very like *D. iulia,* cannot really be judged from observations on a single individual, but it seems probable that its behavior in selecting a site for pupation is more like that of *H. erato* than *D. iulia.*

H. melpomene, H. ricini and to a lesser extent *H. erato* show clear similarities in their choice of pupation site. This is not surprising since they have shared characteristics of feeding and resting. There is little information on *H. sara* and because I did not see the behavior myself, I feel unable to comment on it. There is no evidence to suggest that it should be considered different from *H. melpomene* in its choice of pupation site.

If it were assumed, then, that leaf surfaces were the pupation site among primitive heliconiines and in particular the midrib of the leaf, the situation has changed in *D. iulia, D. phaetusa, H. erato, A. vanillae* and *D. juno.* The argument relating to scarcity of leaves and their flimsiness and flexibility on *P. tuberosa* might explain the abandoning of the presumed primitive site in the cases of *D. iulia, D. phaetusa* and *H. erato.* Much of the manner of eating, position and posture in feeding and resting as well as position during molting has already been related to characteristics of this vine. It might be possible to extend the argument to cover *A. vanillae* as well, in that its food plant *P. foetida,* has fairly thin leaves. *D. juno,* which pupates as a group, could perhaps have been forced into abandoning leaves as pupational sites because of lack of available space. It seems more reasonable, however, to suggest that midrib selection is a specialization adopted within the genus *Heliconius* and that the more basic choice was wider, including stem, petiole, flower stalk and midrib. The tendency to orient with respect to the midrib is particularly strong when the latter is as defined as that in a leaf of *P. laurifolia.* It has already been pointed out that *H. melpomene* and the solitary *H. ricini* and *H. sara* orient to the midrib in feeding, rest along it and molt on it.

If *H. aliphera* were "in the course of" abandoning a preference for protuberances in favor of flat surfaces as pupation sites, a shift to the midrib or a fine vein would be the last stage before reaching a leaf blade position like that of *H. isabella.*

In other prepupational behavior *H. aliphera*

and *H. isabella* are distinct from *H. melpomene*, *H. erato*, *H. ricini* and *H. sara*. They eat until the search for a pupation site begins and *H. isabella* may even stop to eat during the walk. The search begins distinctly later in the day than it does among other *Heliconius* species. Differences in "trying for height" behavior are almost certainly part of a syndrome of pupal adaptation and adult emergence and in all this *H. aliphera* and *H. isabella* are alike and differ from other *Heliconius*. The significance of the color differences in the silk of the pupal pads is obscure. It is worth noticing, however, that *H. aliphera* and *H. isabella* again resemble each other in producing white silk and in differing from *H. melpomene*, *H. erato* and *H. ricini*. The red or pink silk characteristic of these latter species is certainly a specialization in that *D. iulia, D. phaetusa, D. juno, A. vanillae* and even *H. sara* produce white silk like that of *H. aliphera* and *H. isabella*.

D. iulia, D. phaetusa and especially *D. juno* select their sites late in the day. *A. vanillae*, on the other hand, has usually chosen its site and often hung up by mid- or late afternoon, only slightly later than is usual for *H. aliphera* and *H. isabella*. It spends an even longer period between its last larval feed and the time when it hangs up, sometimes resting almost motionless from 6:30 a.m. until the afternoon. A long fast also occurs in *D. iulia* but since fifth instar caterpillars of this species do not normally feed during the morning, its relation to the fast in *A. vanillae* is not clear. Among lepidoptera in general it seems that pupational behavior only starts some time after the last larval meal—thus Crowell (1943) describes a protracted resting period in *Prodenia* larvae prior to pupation and the larvae of the cecropia silk moth do not begin their wandering phase until they have emptied their guts of the last larval meal (v.d. Kloot & Williams, 1953). This would support the idea that *H. aliphera* and *H. isabella* are specialized in having no rest period at all prior to site selection and that *A. vanillae* is in this respect the most primitive of the species considered here.

The time of day at which a pupating caterpillar sheds its last larval skin is linked at least partially with the time at which it spun its pad and hung up on the day before. Thus *H. erato, H. melpomene* and *H. ricini* tend to be earliest. *H. aliphera, H. isabella, A. vanillae* and *D. iulia* are somewhat later. *D. juno* is the latest and here the last larval skins are still being shed during mid-afternoon of the day after hanging up.

Among the behavioral characteristics of the pupa itself, those of *H. isabella* and *H. aliphera* again are in an association separating them

sharply from *H. melpomene, H. ricini, H. erato, D. iulia* and *D. phaetusa*, though less strongly from *A. vanillae* and *D. juno*. The two species mentioned last are perhaps more closely allied to each other in their pupal than in any other behavior.

The behavior described for *H. melpomene* and *D. iulia* so far has been fairly distinct. In pupal behavior, however, they are very alike, movements, sounds and odor production being very similar. The odors are perhaps different enough to suggest that this might be due to convergence. Yet it has already been pointed out that *D. iulia* might be losing the gold spots which are suggested as part of the equipment of advertisement. The direction of evolution in such a case can only be estimated in the light of other closely related species. It is thus very unfortunate that information on pupal behavior of *D. phaetusa* is so limited as to be valueless in such a connection. Since this species so often shows characteristics intermediate between those of *D. iulia* and the *Heliconius* species, it might well be of importance here.

The close relationship of *H. ricini* and *H. erato* with each other and with *H. melpomene* has been continually evident throughout the study and these two species are so alike in pupal behavior and form that it is possible to confuse them.

Information on the emergence behavior of the species is admittedly scanty, yet it is sufficient to divide the butterflies into four groups.

H. melpomene, H. erato, H. ricini and *H. sara* compose the first of these. All of the four show palp movements clearly during the wing fanning phase of emergence but lack them altogether during the subsequent relaxation. None of them extend the palps or twist their heads from side to side just prior to flight. The actual fanning phase is variable, both in duration and number of wing beats. With the exception of *H. sara*, however, the range of variation of this group would have to be extended to accommodate any of the other species studied in Trinidad. The rate of wing beating is very close in *H. melpomene, H. erato* and *H. ricini*, though *H. sara* beats very much faster.

H. aliphera and *H. isabella* are closer to the other *Heliconius* in the emergence behavior of their imagos than any other aspects so far. Movement of the palps during fanning is however less marked and tends to occur later. There is also a slight tendency to include palp movements in the relaxation period. The wing beats of fanning are somewhat quicker in the other *Heliconius* but the duration of the behavior is the same.

The six species considered so far show no sign of palp twitching and twisting of the head before flight but all of the remaining species do. Of these *D. iulia* and *D. phaetusa* form one group, *A. vanillae* and *D. juno* the other. The former are like the four *Heliconius* species in that palp movement is obvious during fanning and does not extend into the relaxation period. The rate of fanning in *D. phaetusa* is approximately the same as that in the *H. melpomene* group, but in *D. iulia* it is much higher.

Both *D. juno* and *A. vanillae* show practically no palp movement during fanning but have a very distinct burst of it during relaxation. The wing beats during fanning are much slower than in any other species.

Information relating to the period between emergence from the pupal case and shedding of the meconium is surprising. Firstly because the co-efficient of variation varies so much between species, being very high in *H. melpomene* and *H. erato* and only an eighth the size in *D. juno* and *A. vanillae*. It seems possible that the point at which meconium is shed is changing in some species or that an unsuspected feature, such as the sex of the individual, is coming into the matter.

The second point for comment is that the time of shedding meconium differs so between species which would be regarded as closely related on other grounds. Thus *D. iulia* and *D. phaetusa* contrast strongly, as do *H. aliphera* and *H. isabella*. Since the liberation of meconium is not effected by whether or not fanning occurs, it is logical that the point of time at which it occurs bears no relation to duration or rate of fanning. Nor is there any direct correlation between the color of meconium and time of shedding.

Consideration of the color of the meconium supports all previous evidence linking *H. aliphera* and *H. isabella* and separating them from the other species of *Heliconius*. This character also links *D. juno* and *A. vanillae* as do other features of their larval and pupal behavior. Meconium of *D. iulia* and *D. phaetusa* cannot be distinguished by color. All of the remaining species of *Heliconius* clearly belong together as a group for, although *H. ricini* produces none of the gray meconium typical of the others, it is nevertheless closer to *H. melpomene* than to any other species in respect of color.

In conclusion, much of the information given in this paper supports the hypotheses raised tentatively in the discussion of Part I. Relationships gauged on general behavior of the caterpillars corresponds fairly closely with those suggested by considering larval molting, and the behavior of pupae and emerging adults. It is interesting, however, that the apparent degree of relationship between species differs at different stages. Thus the early larval instars of *H. aliphera*, *H. isabella* and *D. juno* are very alike in their feeding patterns. As they grow, similarities decrease. Pupal behavior is distinctly different and the question arises as to whether the points of agreement could not be due to convergence. The behavior of emergent *H. aliphera* and *H. isabella* is no closer to that of *D. juno* than any other species. Conversely, the relationship between these two species of *Heliconius* and the *H. melpomene*, *H. erato*, *H. ricini*, *H. sara* group is extremely obscure during larval and pupal life and it is only at the emergence of the adult that similarities become apparent.

The last mentioned group of *Heliconius* may indeed warrent Michener's description of "large and relatively homogeneous" (1942) in adult behavior but among the larvae there are at least some cases of non-conformity. Thus *H. erato*, on the basis of late larval, pupal and emergent behavior, is obviously closely related to *H. melpomene*. In its general larval behavior, however, even including molting, this is masked by modifications which probably arose in relation to its particular food plant. There are indications that it may originally have lived on a vine other than its present *P. tuberosa* and it has been suggested that this was somewhat like the thick-veined *P. laurifolia* on which *H. melpomene* and *H. ricini* feed.

Thus the behavior of larval lepidoptera can clearly be of taxonomic significance. The point which is perhaps of more importance is that such behavioral features, together with those of pupal and adult stages, are essential to form a picture of evolutionary relationships which is anywhere near complete. Taxonomists once favored the use of characteristics which are as far as possible independent of the environment, preferentially those with no apparent functional significance: in the past features which could be regarded as adaptive have been taxonomically suspect. There is now a wider recognition of the fact that to understand the pathway along which an animal has evolved, its mode of life, in as many aspects as possible, must be considered. While nobody is ever likely to suggest that animals be classified on their behavioral characteristics alone, or on their physiology, biochemistry or ecology, such disciplines are essential in interpreting anatomical features.

VII. Summary

1. Behavioral observations were made on cater-

pillars of butterflies of the subfamily Heliconiinae. Some of these observations concern 11 of the 14 species present in Trinidad, some concern 10 and some 9.

2. A brief description is given of the general molting behavior. This comprises a quiescent period, the movements during the actual shedding of the skin, expansion of the scoli, hardening and darkening of the cuticle and a further period of rest. The larva then turns to eat its cast skin before resuming normal feeding. Slight systematic differences occurring within the behavior are described.

3. It is established that caterpillars will eat several cast skins, one after the other, and that they do not distinguish between those of their own and other species. The age of the exuvium is of no significance but that of a fifth instar animal, *i.e.*, last larval molt, is usually rejected.

4. Behavior leading to the selection of a pupation site is described. This involves a locomotory phase and some estimation of the amount of free space beneath a potential site. Differences in the preferred pupation sites of the species are described and the significance briefly considered.

5. Behavior leading to the attachment of a late fifth instar larva to its silk pad is described and the results of experimental interference related. The degree of flexibility of attachment, the extent of movement, stridulation and production of odor are compared in the ten species whose pupae were studied. These features are correlated with pupation site, form and color of the pupae.

6. Emergence of a butterfly from its pupa is described and specific differences in this behavior noted. Observations made when recently emerged butterflies were forced to walk for varying periods before wing expansion are described and the implications of the results are discussed in relation to larval behavior and the pupation site.

7. The phylogenetic implications of the systematic differences in molting, late larval, pupal and emergent adult behavior are discussed. Practically all the information suggests the same picture of the relationship of the species concerned.

This coincides to a great extent with that drawn from considering general larval behavior.

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EXPLANATION OF THE PLATE

PLATE I

Pupa of *H. aliphera,* showing the dorso-ventral bend in the body which causes it to lie almost parallel to the surface under which it is attached, in this case a sheet of glass.